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**NEW EVIDENCE ON THE EVOLUTION OF
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ORIGIN OF THE TETRAPOD LIMB, WITH
DESCRIPTION OF A NEW GENUS OF
OSTEOLEPIDAE**

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NEW EVIDENCE ON THE EVOLUTION OF THE PAIRED FINS OF RHIPIDISTIA AND THE ORIGIN OF THE TETRAPOD LIMB, WITH DESCRIPTION OF A NEW GENUS OF OSTEOLEPIDAE

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ABSTRACT

A specimen of *Sterropterygion brandei*, gen. et sp. nov., a rhipidistian from the Upper Devonian of Pennsylvania, shows for the first time the detailed internal structure of the pectoral and pelvic fins and girdles in a member of the Family Osteolepidae. The structure conforms to the general pattern once thought to be directly antecedent to that of tetrapods but which now must also be considered an ancient feature of rhipidistian fishes. It is contended that the known Rhipidistia could not support their own weight during terrestrial locomotion through fin action alone and a scheme of evolution is proposed according to which the paired fins of osteolepids and tristicopterids evolved with a dual function: in locomotion and support of lung ventilation.

INTRODUCTION

In studies of the fish-tetrapod transition, great attention has been paid to the paired fins and girdles of the ancestral group of fishes — the Devonian Rhipidistia. Andrews and Westoll (1970a,b) have recently summarized our knowledge of the postcranial skeleton of Rhipidistia and contributed greatly to our understanding of the early evolution of the pentadactyl limb. However, all such studies have had to depend heavily upon a single fish — the lowermost Upper Devonian *Eusthenopteron foordi* Whiteaves (Family Tristricteridae, in the classification used by Thomson, 1969) and comparative materials have been scarce. The recent discovery of a well-preserved member of the rhipidistian Family Osteolepidae (Figs. 1-5), showing for the first time both the pectoral and pelvic fins, with girdles, provides an important source of new data.

The specimen with which the present notice is concerned was collected by Mr. Scott Brande at a highway cut outcropping of an Upper Devonian formation in Lycoming County, Pennsylvania. The present preliminary account will be followed at a later date by a full description and analysis. The new osteolepid fish represents a new genus and species. A brief taxonomic diagnosis is necessary.

CLASS OSTEICHTHYES
ORDER CROSSOPTERYGII
FAMILY OSTEOLEPIDAE
Genus *Sterropterygion* nov.

TYPE SPECIES. *Sterropterygion brandei* Thomson, nov.

PRELIMINARY DIAGNOSIS. Rhipidistian with dermal bones and rhomboid scales bearing complete external covering of enameloid and dentine typical of the Osteolepidae. Estimated total length 380 mm. First dorsal fin inserted slightly behind the level of the pelvic insertion, and second dorsal in front of, or level with, the anal. Number of dorsolateral scale rows in front of first

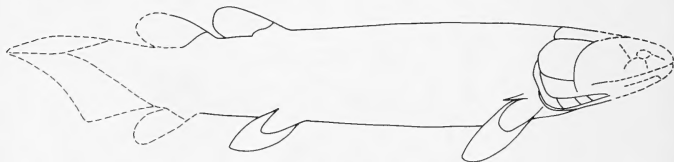


FIG. 1. Reconstruction of the general features of *Sterropterygion brandei* gen. et sp. nov., Holotype.

dorsal, second dorsal and pelvic fins: 41, 53, 50 respectively. Tenth dorso-lateral scale row with 6 scales above and 5 below the lateral line scale. Dorsomedian scale row count: anterior division 41 ± 1 , median division 6; length of anterior division approximately 4.7 times longer than the estimated length of the ethmoidal division of the skull roof.

HORIZON AND LOCALITY. The Upper Devonian Susquehanna Group, probably Catskill Formation, of Northern Lycoming County, Pennsylvania.

DERIVATIO NOMINIS: from the Greek for "firm-fin."

***Sterropterygion brandei* sp. nov.**

HOLOTYPE and sole known specimen: YPM 6721, incomplete fish.

DIAGNOSIS AND OCCURRENCE. As for the genus above.

DERIVATIO NOMINIS: after the discoverer, Mr. Scott Brande.

DISCUSSION

The right pectoral fin of *Sterropterygion brandei* (Fig. 4) is almost complete. The internal fin skeleton consists of a stout humerus with a large entepicondyle, a long thin radius, and a short ulna supporting four more distal elements. The ventral surface of the humerus is marked by a prominent row of projections marking the insertion of the ventral flexor musculature and *M. pectoralis*. The dorsal side bears only moderately developed processes for the insertion of the deltoid muscles. The pectoral fin differs from that of *Eusthenopteron* in that the lobed part occupies just slightly less than half (as opposed to approximately one third) the total length of the fin. In the internal skeleton, the new fish is unique in its short and broad humerus with a massive entepicondylar platform, the specialization of the ventral humeral ridge into a series of large discrete processes for muscle insertion, the slender and elongate radius, and the great breadth of the postaxial elements articulated with the ulna.

The pelvic structures of *Sterropterygion brandei* are shown in Figure 5. The internal fin skeleton differs from that of *Eusthenopteron* in being broader and shorter, particularly in the distal elements. The pelvic fin lobe occupies half the total length of the fin (as opposed to one third in *Eusthenopteron*). The osteolepid pelvic girdle previously has been completely unknown; that of *Sterropterygion brandei* consists of a pair of arch-shaped elements with long anterior iliac processes coming close together in the midline. It is similar to that of *Eusthenopteron*, differing only in the slightly greater breadth of the dorsal public process.

The discovery of *Sterropterygion brandei* reveals the remarkable fact that there are no fundamental points of difference in pectoral or pelvic structure between two families of Rhipidistia, the Osteolepidae and Tristricopteridae, that have been distinct since least the Middle Devonian. (This confirms the observation of Andrews and Westoll, 1970b, based on fragmentary pectoral material of the Carboniferous osteolepid *Megalichthys*.) Moreover, there is evidence that the osteolepids range back to the Lower Devonian (undescribed material from China reported to be in the process of description, several years ago, by Mi-man Chang). From the earliest fossil record of the Rhipidistia there seem to have been two distinct patterns of paired fin development. The holoptychoids (Porolepidae and Holoptychidae) had a monoseriate pattern similar to that of lungfish and coelacanths and it is extremely unlikely that they gave rise to any tetrapods (Schultze, 1970). The biseriate condition seen in osteolepids and tristricopterids is equally ancient and must be considered a primitive, rather than derived, character in these lines. Thus, the biseriate condition of the paired fins, which shows great similarity to that of the Amphibia in the proximal elements (but not the distal elements) must be primarily an adaption for life in water. It is not a specialization of the immediate tetrapod ancestors and it is extremely unlikely that this condition evolved in response to selection involving specific factors of semiterrestrial existence.

The following interpretation of the evolution of the tetrapod limb is suggested by this new evidence. The paired fins of Rhipidistia seem to be adapted primarily for slow swimming movements, much as in the modern lobe-finned chondrosteian *Polypterus*. Presumably, at an early point in their history, the Rhipidistia began to make excursions overland. The possible environmental and adaptive contents have been reviewed by Thomson (1969) and Andrews and Westoll (1970a). But it is extremely doubtful that the pectoral and pelvic limbs were sufficiently developed that these fish could "walk," that is, move through the actions of the paired fins alone. Furthermore, in all known Rhipidistia there was a large fin web that would have been a severe hindrance to attempts at rapid terrestrial movement, primarily by means of limb movements with the fin sharply flexed ventrally to raise the trunk from the ground.

It has been pointed out previously (Thomson, 1969) that, in their experimental movements overland, the prime new mechanical problem facing the lobe-finned fishes was not locomotion but lung ventilation. Locomotion was always possible by lateral body undulation, but lung ventilation required that the anterior trunk (at least) be raised up so that the weight of the body did not crush the lungs. While the pectoral limbs of Rhipidistia do not seem to have been strong enough to contribute greatly to active terrestrial locomotion, they were probably strong enough to lift up the anterior trunk when the animal was at rest. Thus the paired limbs of Rhipidistia may have been subject to two separate selective pressures. First, the fins were used as relatively immobile props in terrestrial locomotion. The mode of progression

was based on the normal sinuous movement of the body, but the trunk musculature could also apply force around the fixed point where each paired fin touched the ground. In this way a lever effect was produced and also the opposite fin was raised off the ground as it was being swung forward. Any addition to this action that could be made by the muscles and skeleton of the fins themselves would be favored. Since this type of locomotion involves a net raising of the trunk, lung ventilation would be facilitated. When the fish was at rest, however, the only means for raising the anterior trunk would be through the direct action of the fins themselves. This would require considerably less strength and mobility than a similar action during active locomotion and perhaps was possible from an early stage in rhipidistian evolution. Any increase in this capacity would be favored, but it is worth noting that the latter function applies more to the pectoral than pelvic fins and this may be a partial explanation of their differential development toward the pentadactyl condition.

Only significantly later (Late Devonian) came reduction of the fin web and further modification of the internal fin skeleton (including development of the carpus and tarsus) allowing greater mobility and more extensive weight support. The robust development of the paired fins in *Sterropterygion brandei* may indicate that it belongs to an advanced stage in this sequence, but it remains essentially a fish and one must expect that the final stages will be found in animals that were more amphibian than piscine in overall organization.

ACKNOWLEDGMENTS

I am deeply grateful to Mr. Scott Brande for his careful collection of the fish and its donation to the Peabody Museum of Natural History. Professor Z. D. Bowen, University of Rochester, also recognized the importance of the specimen and kindly brought it to my attention. The study would not have been possible without the extraordinarily delicate and painstaking preparation by Mr. Peter Whybrow. The photographs were taken by Mr. A. H. Coleman and the study supported by National Science Foundation Grant GB 28823X.

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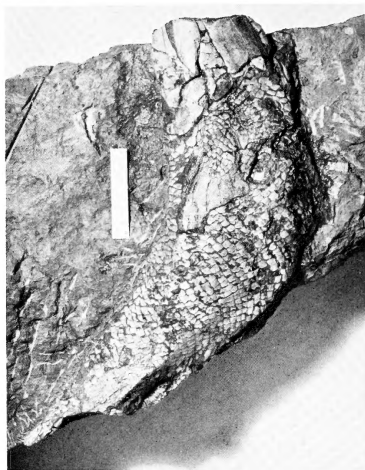


FIG. 2. General view of the right flank of *Sterropterygion brandei* gen. et sp. nov., Holotype. $\times 0.55$.

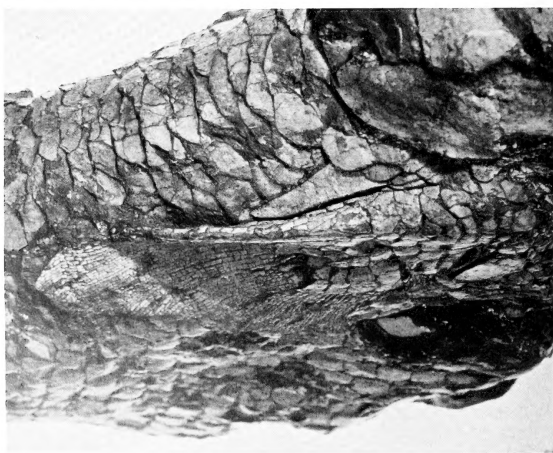


FIG. 3. Detail of the right pectoral fin of *Sterropterygion brandei* gen. et sp. nov., Holotype. $\times 1.2$.



FIG. 4. The pectoral fin of *Sterropterygion brandei* gen. et sp. nov., Holotype. Scales removed to show internal elements, ventral. $\times 1.0$.

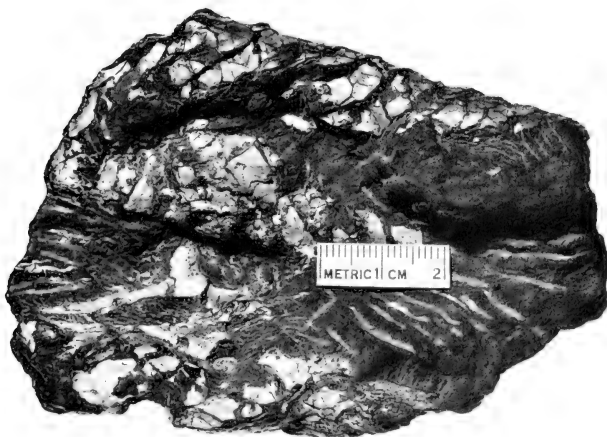


FIG. 5. The pelvic fin and girdle of *Sterropterygion brandei* gen. et sp. nov., Holotype. Prepared specimen showing both girdles and the left pelvic fin. $\times 1.0$.



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